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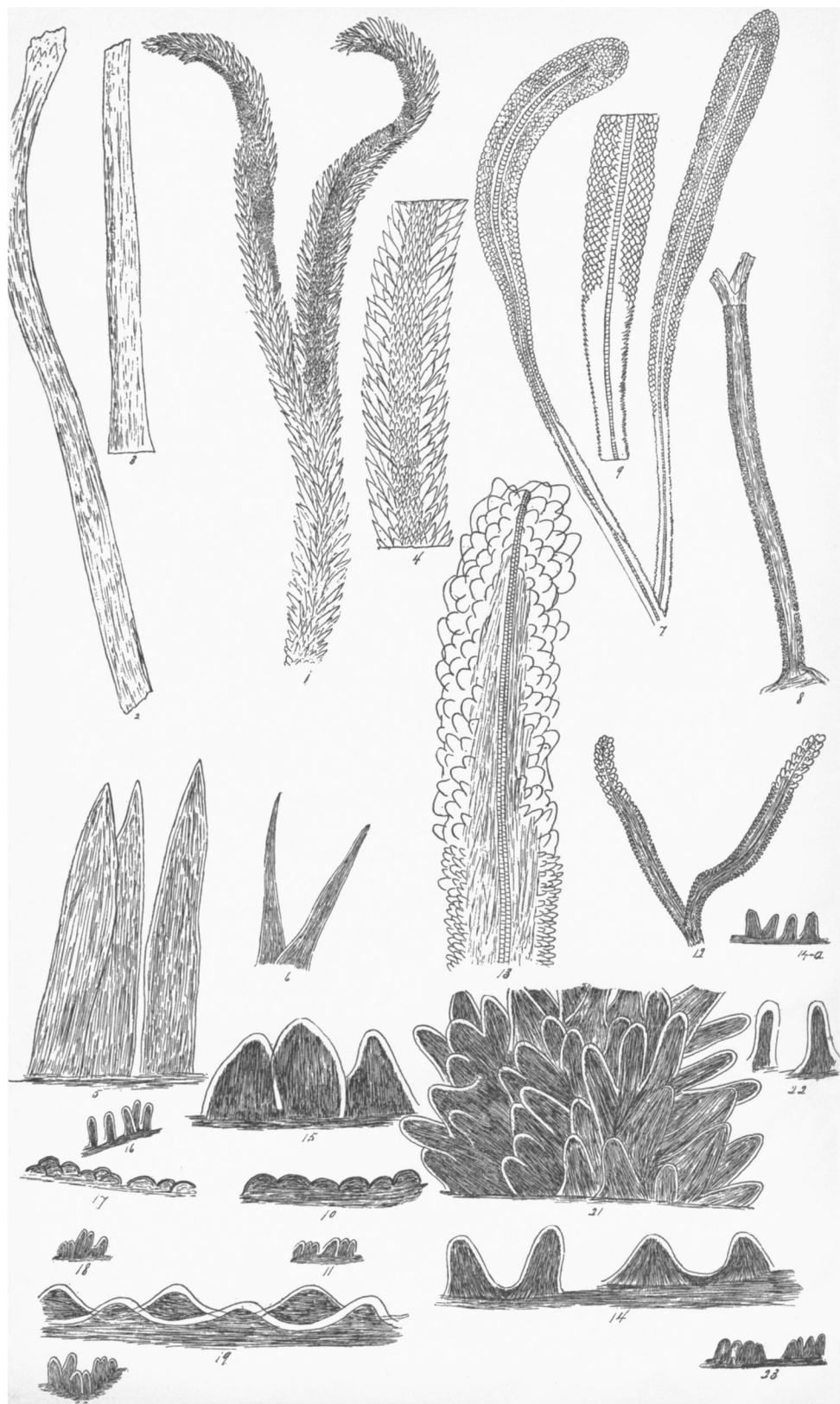
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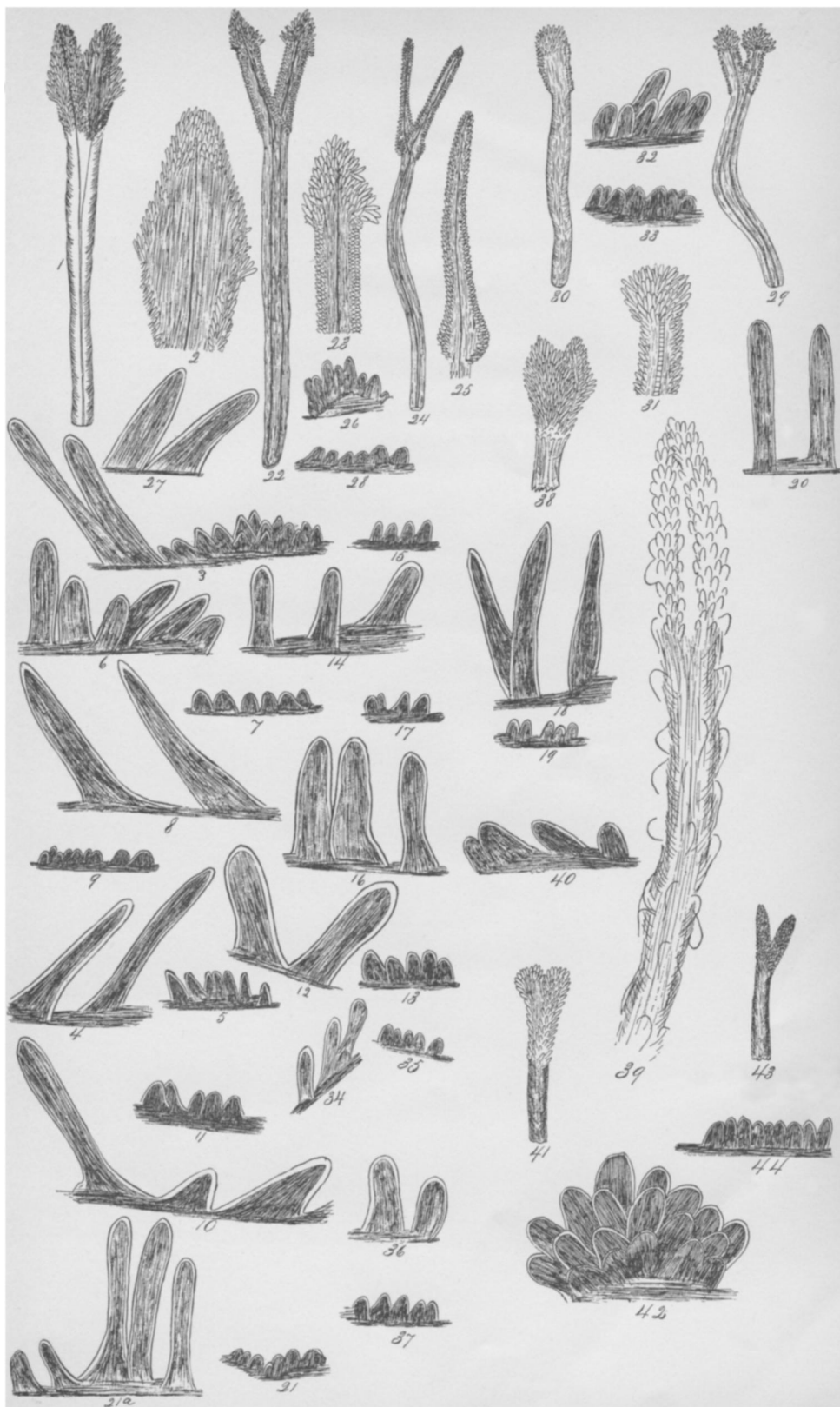
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A Comparative Study of the Styles of Compositæ.*

BY J. S. CHAMBERLAIN.

(Plates CXVII and CXVIII.)

The order Compositæ contains more species than any other order of the flowering plants. Bentham¹ estimated the number of species known to him at nearly ten thousand. They are distributed in seven hundred and fifty genera, collected into thirteen tribes.

The two hundred and thirty-five genera native to North America are distributed in eleven tribes, and according to Dr. Gray² comprise one-eighth of the Phænogams of the continent.

Although the order contains so many species, it is so remarkably distinct and uniform throughout that a species is seldom wrongly referred to or excluded from it.

But to correctly place these ten thousand species in their proper genera, and these in their proper tribes, has been an immense undertaking for systematic botanists. It has been necessary to use characters derived from almost every part of the flower, differences in the inflorescence, corolla, pappus, appendages of the anthers, style, sexual differences, etc., many of which in other orders are considered of only secondary importance.

Linnaeus, who arranged the Compositæ into four great tribes, based his classification on sexual differences. Henri Cassini³ undertook a revision of the order, and in his classification made use of the style characters for the first time. Lessing⁴ and De Candolle⁵ made revisions of the order. They, more than Cassini, made use of the style characters. Great and valuable work has been accomplished by Dr. Gray, who in his various works on North America Botany has made use of the style characters in

* Among the most convenient characters for separating tribes of the Compositæ is the structure of the style, but teachers seldom use this. With the hope that teachers will use this character more generally Mr. Chamberlain has studied in my laboratory the principal tribes and genera in Gray's Manual. The results of his labors are presented here.—L. H. PAMMEL.

¹ Notes on Compositæ, p. 336.

² Synoptical Flora of North America, p. 49.

³ Opusculæ Botaniquæ.

⁴ Syn. Generum Compositarum.

⁵ Prodrômus.

distributing the Compositæ. Bentham⁶ who carefully revised the order for the "Genera Plantarum" after considering all points says: "The style branches of the hermaphrodite florets afford one of the most useful characters for the determination of genera and some tribes; but all attempts to take it as absolute have hitherto miserably failed, and it must always be considered in combination with other characters." The character of the venation of the corolla, used by David Don⁷ and the differences of the achenium used by G. Schultz Bipontinus, were considered of great importance by these authors.

The pappus, which has been used somewhat, is of much greater diagnostic value than the achenium, as it is constant in species and in natural genera and tribes.

The appendages of the anthers, which are attached either to the base or the apex in some genera and tribes, are of some value. Peculiarities of the corolla also furnish characters which are of some importance.

The styles in different genera of the order, deviate sufficiently in structure to enable us to use them for tribal or generic characters, and a study of their structure is the subject of this paper.

The styles of the perfect hermaphrodite flowers of the Compositæ are two-branched and furnished with two kinds of hairs, viz., stigmatic papillæ and brush hairs. The stigmatic papillæ are on the inner face of the style branches, arranged in one line, as in *Vernonia* or *Helianthus*, or in two lines, as in *Helenium* or *Aster*, and extend up from the base of the branches to the tip, as in *Vernonia*, or for only a part of the distance, as in *Eupatorium* and *Aster*. The papillæ are usually short, with either an acute or obtuse tip, but never acuminate.

The brush hairs, or collecting hairs as they are sometimes called, are arranged in several ways, e. g., in a truncate bunch at the tip of the branch, as in *Senecio*; or along the outer face of the branches, extending sometimes below the fork, as in *Vernonia*, and sometimes just to the fork, as in *Solidago*; or covering both faces of the branch above the termination of the stigmatic lines as in *Aster*. The function of the brush hairs is to brush out and collect the pollen from the anther tube.

⁶ L. c.

⁷ Monographs on Compositæ.

Before the flower opens the style branches are closed within the flower. The lines of stigmatic papillæ are closed in against each other on the inner face of the style branches and thus remain unexposed until after the flower opens and the branches separate.

When the flower opens the style pushes up through the anther tube and the brush hairs brush out and collect the pollen as the anthers dehisce.

The pollen thus held by the brush hairs is usually removed by insects before the stigmatic papillæ are exposed. Self-pollination is therefore not likely to occur. As the style grows, the branches separate, often curving far back, and the stigmatic papillæ are in a position to be readily pollinated by insects. By this mechanism cross-pollination of the Compositæ seems almost certain, though self-pollination does occur.

In *Xanthium*, which is anemophilous, the brush hairs are not needed, and consequently they are more or less abortive.

In the female flowers the style is always two-branched, but brush hairs are absent, as they would be useless. The stigmatic papillæ cover the entire inner face of the branches or are arranged in two lines. Some exceptions occur, however, as in *Inula*⁸ where the style of the pistillate ray flowers is like that of the hermaphrodite flowers.

In male flowers the style is either entire or two-branched sometimes both forms occurring in the same genus. The pistil being sterile it has no function to perform except that of removing the pollen from the anther tube, and consequently we find brush hairs but no stigmatic papillæ.

Cassini⁹, Lessing¹⁰, De Candolle¹¹, and Lindley¹², in their classifications seem to have noticed only the variations in the shape of the branches, while the differences in arrangement, size, shape, etc., of the brush hairs and the stigmatic papillæ was unnoticed. Le Maout and Decaisne¹³, Bentham¹⁴ and Gray¹⁵ all notice the brush hairs and stigmatic papillæ to some extent, the latter using them for distinct tribal characters.

⁸ Lubbock :—British Wild Flowers in Relation to Insects, p. 115.

⁹ L. c. ¹⁰ L. c. ¹¹ L. c. ¹² Flora Medica, p. 450.

¹³ Descriptive Botany, p. 497.

¹⁴ L. c., p. 349. ¹⁵ L. c., p. 49.

F. Hildebrand¹⁶, who has given a thorough description, with plates, of the genera studied by him, notices the brush hairs and stigmatic papillæ closely, the purpose of his paper being to point out the mechanism for pollination.

Bentham and Hooker in "Genera Plantarum" divide the order Compositæ into thirteen tribes, of which ten are included in the revised edition of Gray's New Manual, as follows: 1 *Vernoniaceæ*, 2 *Eupatoriaceæ*, 3 *Asteroideæ*, 4 *Inuloideæ*, 5 *Helianthoideæ*, 6 *Helenioideæ*, 7 *Anthemideæ*, 8 *Senecionideæ*, 9 *Cynaroideæ*, 10 *Cichoriaceæ*. In Gray's "Synoptical Flora of North America" one other tribe is given, viz: *Mutisiaceæ*. In the arrangement of tribes I have followed Gray. In most cases the genera in each tribe are taken up as they appear in the Manual.

VERNONIACEÆ (plate CXVII fig 1-6).

Of the Vernoniaceæ Gray says: "Style branches slender, filiform or attenuate subulate, acute, hispidulous or hispid; stigmatic lines only near the base."

Bentham says: "Stigmatic lines near the base on the inner surface not very conspicuous."

I do not, however, find the arrangement of the stigmatic papillæ as they are described by these authors.

In *Vernonia* and *Elephantopus*, the stigmatic papillæ are arranged in one line, occupying about one-third of the inner face of the branches and extending up the center of this face from the base to within a very short distance of the tip.

This is nearly as Hildebrand¹⁷ has described it except that a single stigmatic line occupies the whole inner face. The stigmatic lines are very distinct and are essentially the same in *Vernonia* and *Elephantopus*. The papillæ in both genera are short, broad at the base and taper to an acute point. The brush hairs cover the entire surface not covered by papillæ and extend for some distance below the forks.

*Vernonia*¹⁸ (Fig. 1-5).

V. Arkansana, DC. The branches of the style are terete, long, (about one-fourth the length of the style)

¹⁶ Ueber die Geschlechtsverhältnisse bei den Compositen.

¹⁷ L. c., p. 14.

¹⁸ Hildebrand l. c., p. 14. Cassini l. c., p. 22.

slender, tapering gradually to an acute tip. The arrangement of papillæ and hairs is as described for the tribe. The brush hairs (fig. 5) are large, linear and taper to an acute tip. They extend below the forks about two-thirds the length of the branches and cover the surface thickly.

Elephantopus (Fig. 6).

E. Carolinianus, Willd. The branches of the style are much like those of *Vernonia* except in an obtuse tip. The brush hairs (fig. 6) taper rapidly to an acuminate tip and are only about one-half the length of those of *Vernonia Arkansana*. The brush hairs extend below the forks for only about one-fourth the length of the branches.

EUPATORIACEÆ (plate CXVII, fig. 7-23).

Gray¹⁹ says: "Style branches elongated, more or less clavate or thickened upward, minutely papillose or puberulose or glabrous; the stigmatic lines only near the base and inconspicuous."

In three of the six genera studied the style was very plainly club-shaped. In the others it was merely more cylindrical above the end of the stigmatic lines. The clavate character of the branches is, therefore, not uniform for all the genera of the tribe, as stated by some. They are either clavate or mostly cylindrical above. Stigmatic lines only near the base is true in most cases.

In some genera, however, as in *Mikania*, the stigmatic lines extend up for more than two-thirds the distance. A uniform character was, however, found in all six genera studied, namely, the stigmatic lines are always very narrow along the outer edges of the branches and the brush hairs cover the entire surface or the greater part of it above the end of the stigmatic lines.

Kuhnia (Fig. 7-11).

K. eupatorioides, L. Style branches distinctly club-shaped, as shown in figs. 7-9. The stigmatic papillæ (fig. 11) are arranged in two narrow lines along the edges of the branches and occupy the lower three-sevenths of the branches. The papillæ are moderately large and acute. The brush hairs (fig. 10) cover almost the entire surface above the end of the stigmatic lines. They are very obtuse and broad.

¹⁹ L. c., p. 51.

Mikania (Fig. 12-14a).

M. scandens, (L.) Willd. Style branches (fig. 12-13) are not clavate as in *Kuhnia*, but are cylindrical above the end of the stigmatic lines. The stigmatic papillæ (fig. 14a) are arranged in two lines as in *Kuhnia*, but are wider and occupy fully two-thirds of the length of the branch. In shape they differ only slightly from *Kuhnia*. The brush hairs (fig. 14) are larger and more acute than in *Kuhnia*. They do not cover the entire surface, but leave a narrow uncovered portion along the center of the branch.

*Eupatorium*²⁰ (Fig. 15-16).

Eupatorium altissimum, L. The style branches are distinctly clavate. Stigmatic papillæ (fig. 16) are arranged as in *Kuhnia* and occupy the lower two-fifths of the branch. The brush hairs (fig. 15) cover nearly the entire surface above the end of the stigmatic lines. The largest hairs are just above the end of the stigmatic lines.

According to Cassini, as quoted by Hildebrand, the styles of *Eupatorium purpureum*, *E. sessilifolium*, and *E. altissimum* are like *Eupatorium cannabinum*.

Brickellia (Fig. 17-18).

B. Wrightii, Gray, var. *tenera*, Gray. The style branches are nearly like those of *Kuhnia*, only becoming more gradually clavate, while the tip is more acute. Stigmatic papillæ (fig. 18) are nearly like those of *Kuhnia* in shape, size and arrangement. The brush hairs (fig. 17) are like those of *Kuhnia* in all respects.

Liatris (Fig. 19-20).

L. squarrosa, (L.) Willd. The style branches are not clavate, but the upper part is very long and cylindrical. The stigmatic lines, which are very narrow at the base of the branches, become somewhat broader before they terminate. They occupy only about one-third of the length of the branch (fig. 20). The brush hairs are arranged as in the other genera. In the full grown style they are broad at the base, and taper to a rather acute point (fig. 19). According to Hildebrand²¹ they are long and slender before the flower opens, later they become broader at the base, but do not grow in length.

²⁰ Hildebrand l. c., p., 16.

²¹ L. c., p. 17.

Trilisia (Fig. 21-23).

T. paniculata (Walt.) Cass. Style branches not clavate but cylindrical longer and more acute than in *Mikania*. Stigmatic papillæ (fig. 23) about the same as in *Mikania*, but occupy only one-third of the branch, and are in slightly narrower lines. Brush hairs (fig. 21, 22) cover the entire surface above the stigmatic lines.

ASTEROIDEÆ (plate CXVIII, fig. 1-38).

Gray²⁴ describes the style as follows: "Style branches of hermaphrodite flowers flattened, conspicuously margined by the stigmatic lines and extending into a hispid or papillose (sometimes very short) appendage."

The following genera have been studied: *Grindelia*, *Heterotheca*, *Chrysopsis*, *Aplopappus*, *Bigelovia*, *Solidago*, *Brachychæta*, *Bellis*, *Townsendia*, *Sericocarpus*, *Aphanostephus*, *Boltonia*, *Aster*, *Erigeron* and *Baccharis*.

In all these the style agrees with the description given by Dr. Gray for the tribe. There is a difference, however, in the arrangement of the stigmatic papillæ and brush hairs that makes the following division of the tribe possible, so far as my studies have extended.

DIVISION I.

Style branches of the hermaphrodite flowers flattened, tapering from the base or just above the base to an acute or obtuse point. The stigmatic lines are distinct in two lines along the outer edges and tip. They occupy not more than one-half of the branch. The brush hairs covering the outer surface extending down between the stigmatic lines or leaving an unoccupied space along the center. The inner face is not covered with brush hairs except at the very tip and along the edges. This subdivision includes the genera: *Solidago*, *Grindelia*, *Heterotheca*, *Chrysopsis*, *Aplopappus*, *Bigelovia*, *Brachychæta*, *Bellis*, *Townsendia* and *Sericocarpus*.

DIVISION II.

Style branches flattened, linear from the base to the end of the stigmatic lines. Stigmatic papillæ in two lines as in (I), but

²⁴ L. c. p. 52.

occupying more than one-half of the length of the branch. The brush hairs forming a triangular appendage at the end of the stigmatic lines and nearly equally covering both faces of the branch. The hairs on the outer face extend only a short distance below the end of the stigmatic lines. This subdivision includes the genera *Aster*, *Aphanostephus*, *Erigeron* and *Boltonia*. *Baccharis* has both staminate and pistillate flowers, and does not belong to either of the above.

*Solidago*²³ (plate CXVIII, fig. 1-3).

S. Canadensis, L. The general characters of the style have been given in the description of subdivision I. The stigmatic lines extend up a little less than one-half of the distance to the tip (fig. 1, 2). The brush hairs cover the entire outer surface, and the tip and edges of the inner face above the stigmatic lines (fig. 1, 2). Stigmatic papillæ short, acute. Brush hairs long, cylindrical and obtuse. The shape and relative size of both papillæ and hairs is shown in figure 3.

*Grindelia*²⁵ (Fig. 4, 5).

G. squarrosa (Pursh), Dunal. Style branches much like *Solidago*, only longer and not as broad, gradually tapering to an obtuse point. Stigmatic lines occupy one-half of the length of the branch. Stigmatic papillæ (fig. 5) more slender than in *Solidago*. Brush hairs (fig. 4) do not extend as far down the back as in *Solidago*.

*Heterotheca*²⁶ (Fig. 6, 7).

H. subaxillaris (Lam.), Britt. Style branches enlarged at the base and tapering to a smaller point than in *Solidago* or *Grindelia*. Stigmatic lines occupy one-half of branch. Brush hairs do not occupy outer or inner face entirely, but leave a narrow zone along the center of both faces. Stigmatic papillæ shorter and more obtuse than in *Solidago* (fig. 7). Brush hairs broader and shorter (fig. 6).

*Chrysopsis*²⁴ (Fig. 8, 9).

C. villosa (Pursh), Nutt. Style branches almost identical with

²³ Hildebrand, l. c., p. 22. Müller, l. c., p. 320.

²⁵ Gray, l. c., p. 53.

²⁶ Gray, l. c., p. 53.

²⁴ L. c., p. 53.

those of *Heterotheca*. The brush hairs (fig. 9) are arranged as in *Heterotheca*. The papillæ (fig. 8) are arranged similarly, but are longer and more acuminate.

Aplopappus (Fig. 10, 11).

A. racemosus (Nutt.), Torr. Style branches longer and more tapering than in *Solidago*. Stigmatic papillæ (fig. 11) are about the same shape as in *Solidago*, and occupy one-third of the branch. The brush hairs (fig. 10) are of very different lengths, the largest being larger than any others in the tribe.

Bigelovia (Fig. 12, 13).

B. nudata (Michx.), DC. Style branches slightly broader than in *Heterotheca*. The stigmatic lines occupy hardly one-half of the branch. The papillæ (fig. 13) about as in *Solidago*. Brush hairs (fig. 12) broad and obtuse.

Brachychæta (Fig. 14, 15).

B. cordata (Short), Torr. & Gray. Branches of the style short and obtusely pointed. Stigmatic lines occupy one-third of the branch. The papillæ (fig. 15) are smaller than in *Solidago*. Brush hairs (fig. 14) broader and shorter.

*Bellis*²⁷ (Fig. 16, 17).

B. integrifolia, Michx. Style branches essentially as in *Solidago*. Stigmatic lines occupy a little more than one-third of the branch. The papillæ (fig. 17) are smaller than in *Solidago*, while the brush hairs (fig. 16) are broader and shorter.

*Townsendia*²⁸ (Fig. 18, 19).

T. eximia, Gray. Style branches long and tapering. Stigmatic lines occupying one half of branch. The papillæ (fig. 19) are smaller than in *Solidago*. Brush hairs (fig. 18) acuminate as in *Chrysopsis*.

*Sericocarpus*²⁹ (Fig. 21, 21a).

S. asteroides, (L.) B.S.P. Styles branches very long and slender, about twice the length of *Solidago*. Stigmatic lines occupy about one-fourth of the branch. See figure 21 for papillæ. The brush hairs are shown at figure 21a.

²⁷ Gray, l. c., p. 55. Müller, l. c., p. 321. Hildebrand, l. c., p. 23.

²⁸ Gray, l. c., p. 56.

Gray, l. c., p. 56.

DIVISION II.

*Aster*³⁰ (plate CXVIII, fig. 22-28).

A. Novæ-Angliæ, L. The style branches of the hermaphrodite flowers are about the same length as those of *Solidago*, but are flattened and much narrower. The stigmatic lines are broader and more distinct than in the first division. They occupy two-thirds of the branch. The branches are linear to the end of the stigmatic lines; above this portion of the branch the brush hairs form a triangular appendage, the hairs almost covering both faces, extending down somewhat between the lines on the outer face (fig. 22, 23). The papillæ (fig. 28) are short and obtuse. Brush hairs (fig. 27) are rather short and broad. The style branches of the pistillate ray flowers are narrow and acuminate, while the papillæ occur in two lines along the edges, the brush hairs being absent (fig. 24-26).

Erigeron (Fig. 29-33).

E. Philadelphicus, L. Style branches about one-half as long as in *Aster*. Stigmatic lines occupy two-thirds of the branch, brush hairs covering both faces above the end of the stigmatic lines and forming a triangular appendage (fig. 29-31). The stigmatic lines are narrower and the papillæ larger than in *Aster* (fig. 33). Brush hairs are shorter and more obtuse (fig. 32).

*Aphanostephus*³¹ (Fig. 34, 35).

A. ramosissimus, DC. Style branches like those of *Erigeron*, but only half as long. Stigmatic lines occupy three-fourths of branch. The appendage of the brush hairs is very short. The papillæ are smaller than in *Erigeron* (fig. 35), whereas the brush hairs are narrower and more obtuse (fig. 34).

*Boltonia*³² (Fig. 36, 37).

B. asteroides (L.) L'Her. Style branches very broad in proportion to their length, being about one-third as broad as they are long. In length they are like those of *Erigeron*. Stigmatic lines occupy four-fifths of the branch. The brush hairs form a mucronate-pointed appendage. The papillæ (fig. 37) and brush hairs (fig. 36) are nearly like those of *Erigeron*.

³⁰ Gray, l. c., p. 56.

³¹ Gray, l. c., p. 55.

³² Gray, l. c., p. 56.

*Baccharis*³³ (Fig. 20, 38).

B. halimifolia, L. Style branches of the staminate flower are shown in figure 38. The entire outer face and edges of the inner are covered with brush hairs. Stigmatic papillæ do not occur on the remainder of the inner face. The brush hairs are cylindrical, obtuse (fig. 20).

The branches of the pistillate flowers are twice as long as in the staminate. They are linear in shape, with an acute point. The papillæ occur in two narrow lines along the edges.

INULOIDEÆ³⁴ (plate CXVIII, figs. 39-44).

In this tribe the heads are heterogamous or dioeciously homogamous, and the style, therefore, in most cases, does not possess both brush hairs and stigmatic papillæ; the relative arrangement of the brush hairs cannot therefore be used as a distinctive character. The style of the hermaphrodite sterile flowers is either two-branched or entire. The style of the pistillate flowers is two-branched, but there is no variation in the arrangement of the papillæ. Gray says: "The style branches of the hermaphrodite flowers are flattish or filiform, not appendaged."

*Pluchea*³⁵ (Figs. 39, 40).

P. camphorata, (L.) DC. The style of the hermaphrodite sterile flowers is entire or two-cleft. The branches of the two-cleft style are terete, short in proportion to their length. The brush hairs cover the entire outer surface of the branches. Below the base of the branches the style is covered with glands (fig. 39). The brush hairs (fig. 40) are short and obtuse. The style of the pistillate florets is two-branched, with both faces covered, or nearly so, with papillæ.

*Antennaria*³⁶ (Figs. 41-44).

A. plantaginifolia (L.), Hook. The style of the staminate flowers is two-cleft or entire. The branches of the two-cleft style are somewhat clavate, covered over the outer face and edges of the inner with brush hairs. The remainder of the inner face does not

³³ Gray, l. c., p. 57.

³⁴ Gray, l. c., p. 57. Bentham, l. c., p. 377. Lubbock, l. c., p. 115. Hildebrand, l. c., p. 40.

³⁵ Gray, l. c., p. 57.

³⁶ Gray, l. c., p. 58.

possess stigmatic papillæ (fig. 41). The brush hairs (fig. 42) are short and obtuse. The style of the pistillate flowers is two-cleft. The branches are slightly tapering, the stigmatic papillæ cover the greater part of both faces (fig. 43). The papillæ are small and obtuse (fig. 44).

(*To be continued*).

Notes on the Flora of North Carolina.

BY A. A. HELLER.

The morning of June 19, 1890, found me in the "Old North State," whither my imagination for many months past had carried me almost daily.

On the road to my headquarters near Heilig's Mill post-office, twelve miles south of Salisbury, many things besides the heat of the sun indicated that I was in a part of the world which was new to me.

Ripe blackberries in June were a novelty, and one that claimed my attention from an internal point of view. Great bunches of the brick-red flowers of *Tecoma radicans*, Juss., were plentiful along the road, and so were those of the pretty, purple-rayed *Passiflora incarnata*, L. But the prettiest of all was *Schrankia angustata*, T. and G., with its heads of pink flowers.

On the 20th I did my first collecting, on the road from Salisbury to Heilig's Mill. *Polygala Curtissii*, Gray, was just coming into bloom, and a few plants of *Silene Virginica*, L., and *Asclepias verticillata*, L., were found. A plentiful supply of *Bupleurum rotundifolium*, L., was obtained at one place, and a stop of a few minutes at the "Rocks," six miles south of Salisbury, added *Ilysanthes refracta*, Benth., and *Utricularia cornuta*, Mx., to my list.

On the 21st I made an expedition with the "Parson" to his Bear Creek congregation, twelve miles farther south, and while he was dispensing spiritual food in the shape of catechism, I explored the vicinity. Some of the more important results were: A fruiting specimen of *Rhododendron calendulaceum* (Michx.) Torr. *Coreopsis senifolia*, Mx., which was plentiful, several specimens each of *Clitoria Mariana*, L., and the short, erect form of *Tephrosia*